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CHROMOSOME NUMBERS, APOMIXIS, AND INTERSPECIFIC HYBRIDIZATION IN THE GENUS TOWNSENDIA[1]

John H. Beaman

The genus *Townsendia* Hooker, of the tribe Astereae of the Compositae, consists of about twenty species of small annual, biennial, or perennial, western North American plants. The genus was revised by Larsen (1927), but since that time several poorly understood taxonomic complexes have become apparent. Since no chromosome studies on any member of the genus had previously been reported, a cytotaxonomic study was initiated in an attempt to solve some of these problems through a better understanding of natural relationships within the genus.

As the study progressed, other problems, chiefly involving apomixis and polyploidy, were encountered. With the appearance of these complications came the realization that *Townsendia* is ideally suited for intensive studies directed toward a further understanding of the roles of hybridization, apomixis, and polyploidy in speciation. The genus has a relatively small number of species and a fairly limited range. Most species flower profusely and can be grown without difficulty in the greenhouse or garden. These advantages make it a convenient subject for experimental studies on some of the mechanics of evolution.

Material and Methods

The collections studied are listed by species in Table 1. Culture number, chromosome number, and source of collection are given. Voucher specimens are filed in the Herbarium of the State College of Washington.

The collections were grown in the greenhouse and most of them also in the experimental garden at Pullman, Washington. Seeds were germinated on moist filter paper in petri dishes, the young seedlings transferred to pots, and some of them later transplanted to the garden. Plants of some collections were transplanted from their natural habitat to the greenhouse

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TABLE 1. CHROMOSOME NUMBER AND SOURCE OF TOWNSENDIA COLLECTIONS STUDIED.

Taxon	Culture	Chromosome Number, 2n	Source
T. anomala	33	18	WYOMING, Park Co.: near Holm Lodge on Crossed Sabre Ranch, 10 mi. east of the east entrance to Yellowstone National Park, *Beaman and Preece 503.*
T. arizonica	4	18	ARIZONA, Coconino Co.: 9 mi. east of Peach Springs, *Preece and Turner 2609.*
T. arizonica	5	18	ARIZONA, Coconino Co.: 2 mi. east of Ashfork, *Preece and Turner 2617.*
T. exscapa	46	18	ARIZONA, Coconino Co.: 1 mi. south of campgrounds at Park Headquarters, Grand Canyon National Park, *Jones 800.*
T. florifer	1	18	IDAHO, Custer Co.: Highway 93 near Custer-Lemhi Co. line, *Preece and Turner 2389.*
T. florifer	28	18	OREGON, Harney Co.: 3 mi. south of Wagontire, *Ownbey and Preece 3358.*
T. grandiflora	18	18	COLORADO, Larimer Co.: 2 mi. west of Bellvue, *Preece and Turner 2858.*
T. grandiflora	39	18	COLORADO, Boulder Co.: near summit of Flagstaff Mountain, *Beaman and Preece 509.*
T. incana	6	28	COLORADO, Gunnison Co.: 15.6 mi. west of Gunnison on Highway 50, *Preece and Turner 2795.*
T. incana	37	30	WYOMING, Fremont Co.: 16 mi. southeast of Dubois, *Beaman and Preece 507.*
T. leptotes	42	18	COLORADO, Grand Co.: 4.5 mi. west of Kremmling on U. S. Highway 40, *Beaman and Preece 513.*
T. mensana	38	18	WYOMING, Albany Co.: about 12 mi. southeast of Laramie on U. S. Highway 30, *Beaman and Preece 508.*
T. minima	3	27	UTAH, Kane Co.: 5 mi. west of Long Valley Junction on highways 14 and 89, *Preece and Turner 2462.*
T. montana	35	18	WYOMING, Teton Co.: on south side of Teton Pass, *Beaman and Preece 505.*
T. montana	29	36	OREGON, Wallowa Co.: near shore of Ice Lake, 5 mi. southwest of Wallowa Lake, *Beaman and Preece 500.*
T. Parryi	31	18	MONTANA, Park Co.: 8 mi. west of Livingston, *Beaman and Preece 501.*
T. Parryi	8	36	MONTANA, Park Co.: at Cooke Guard Station, near Cooke City, *Ownbey.*
T. Parryi	34	36	WYOMING, Park Co.: near Holm Lodge on Crossed Sabre Ranch, 10 mi. east of the east entrance to Yellowstone National Park, *Beaman and Preece 504.*
T. Rothrockii	44	36	COLORADO, Park Co.: on Hoosier Ridge, *Beaman, Weber, and Preece 516.*
T. spathulata	47	36?	MONTANA, Park Co.: Ram Pasture Mountain, on the Wyoming border, southeast of Cooke City, *Witt 1845.*

and garden. Polyethylene refrigerator bags were used for shipping living plants from the field to the laboratory.

Studies of microsporogenesis were made using buds collected in the field, the greenhouse, or the garden. Buds were fixed in Carnoy's fluid (6 parts absolute alcohol: 3 parts chloroform: 1 part glacial acetic acid) for one hour, then transferred to 70 per cent alcohol where they were stored at about 10°C. until time of examination. Some buds thus stored

have remained in satisfactory condition for eight months. From the 70 per cent alcohol, individual florets were transferred to a drop of aceto-carmine on a slide, macerated with a glass rod, and smeared by the application of considerable pressure to the coverslip.

Root-tip examinations were made from the primary root of germinating seedlings. The technique used for root-tip smear preparations was similar to that outlined by Speese and Baldwin (1952) for leaf smears. Root tips were first placed in water saturated with paradichlorobenzene for two hours, then washed in distilled water and fixed in Carnoy's fluid (3 parts absolute alcohol: 1 part chloroform: 1 part glacial acetic acid). They were stored in the fixative for from one day to two weeks. After fixation the root tips were hydrolyzed in acid alcohol (1 part concentrated hydrochloric acid: 1 part absolute alcohol) for fifteen minutes. After hydrolyzation they were returned to Carnoy's fluid for about fifteen minutes, then smeared in aceto-carmine by the method described above.

Some of the preparations of buds and root tips were made permanent by the method described by Sears (1941).

Iodine-crystal violet smear preparations of anthers and iodine-crystal violet sections of buds and root tips were tried, but satisfactory results were not obtained.

The camera lucida drawings of meiotic chromosomes were made at late prophase or metaphase. Those of mitotic chromosomes were made at metaphase, the only time when they are shortened sufficiently for counting. All drawings were made under an apochromatic oil-immersion lens of N. A. 1.30 and an initial magnification of 1800 times. The magnification of the figures is approximately 900 times.

Observations

Chromosome numbers of $2n = 18$, $2n = 27$, $2n = 28$, $2n = 30$, and $2n = 36$ were found in the genus. This pattern of numbers indicates that the base number of chromosomes for the genus is nine. This fits well in the Astereae, where the base number nine is found also in the related genera *Aster* and *Erigeron*. The apparent exceptions in the regular progression of the polyploid series, found in *T. incana* where $2n=28$ and $2n=30$, will be considered under that species.

In the discussion of the species, first the diploid, then the polyploid taxa are considered. Species in which only root-tip examinations have been made are considered last.

Townsendia arizonica A. Gray. Two collections of this species were studied. Seeds were germinated in December, 1951; and in May, 1952, the plants started flowering. Plants in the greenhouse have flowered almost constantly from that time until the present. Several plants of Culture 5 developed large fasciations.

The plants of both collections were self-sterile. Nine bivalents were observed at metaphase I (fig. 2), and no irregularities were found in microsporogenesis.

Townsendia florifer A. Gray. Two collections of this species were studied. The plants began flowering about four months after seed germination and continued for a period of from two to four months. After that time they died.

The plants were essentially self-sterile, although some viable seeds were produced by selfed plants. Nine bivalents were observd at metaphase I (fig. 3), and no irregularities were found in microsporogenesis.

Townsendia grandiflora Nutt. Two collections of this species were studied. Seeds of Culture 18 were germinated in March, 1952. This species requires a longer time to reach maturity than most other species, and only one plant has yet flowered.

Nine bivalents were observed at metaphase I (fig. 4), and no meiotic irregularities were found. It is not yet known whether the plants are self-fertile or self-sterile.

Plants of Culture 39 were transplanted from the field. None of these have yet flowered. Seeds collected in the field were germinated to supply root tips for examination. In this examination, 18 chromosomes were observed (fig. 11).

Townsendia leptotes (A. Gray) Osterhout. One collection of this species was studied. The plants were transplanted from the field. In the greenhouse the plants initiated buds, but these did not reach the meiotic stage. Buds for examination were obtained from plants grown in the garden.

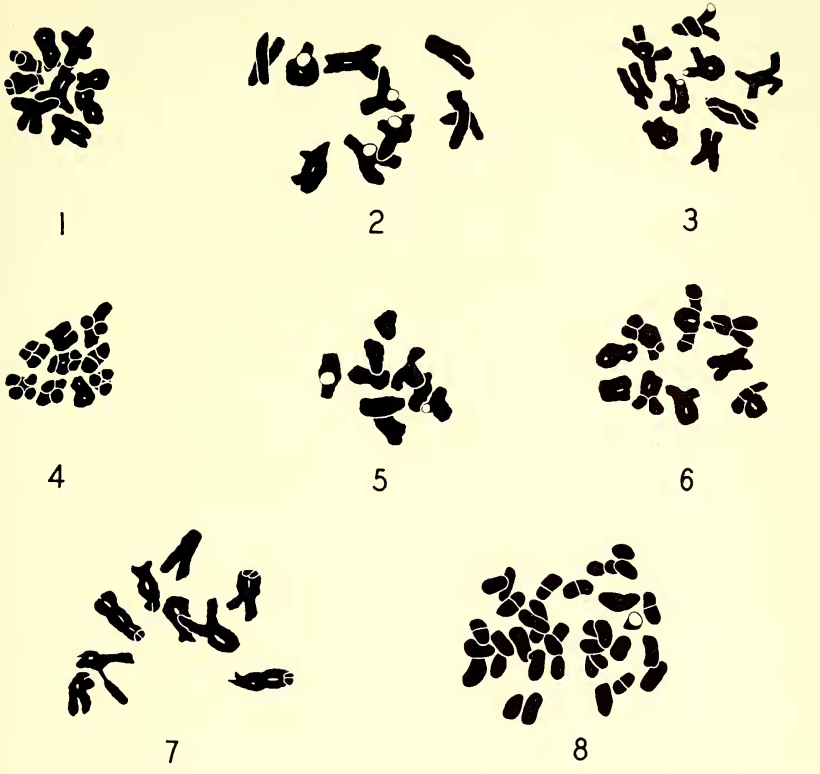
Nine bivalents were observed at metaphase I (fig. 5), and no meiotic irregularities were found. It is not yet known whether the plants are self-fertile or self-sterile.

Townsendia anomala Heiser. One collection of this species was studied. It is from the type locality, the only station from which *T. anomala* is known. Young plants were transplanted from the field. Plants in the greenhouse became much more elongate than those in their natural habitat. This elongation probably resulted from insufficient light, since most growth in the greenhouse took place during the winter. A higher-than-normal water supply in the greenhouse also may have been partially responsible.

These plants were self-sterile. The study of microporogenesis was made from buds collected in the field. Nine bivalents were observed at metaphase I (fig. 1). In a few of the cells examined, chromatin bridges were seen after anaphase II. This irregularity probably indicates inversion of a chromosome segment.

Townsendia mensana M. E. Jones. This species was treated by Larsen (1927) as *T. sericea* Hook., but that name, as originally defined by Hooker, included the type of the earlier *Aster exscapus* Rich. [=*T. exscapa* (Rich.) Porter], and is therefore invalid (Cronquist, unpublished) under Article 65 of the International Code of Botanical Nomenclature.

Several collections of this species were grown in the greenhouse, but,



FIGS. 1–8. Meiotic chromosomes of *Townsendia*. FIG. 1. T. *anomala* (Culture 33). FIG. 2. *T. arizonica* (Culture 4). FIG. 3. *T. florifer* (Culture 28). FIG. 4. *T. grandiflora* (Culture 18). FIG. 5. *T. leptotes* (Culture 42). FIG. 6. *T. mensana* (Culture 38). FIG. 7. *T. montana* (Culture 35). FIG. 8. *T. montana* (Culture 29). All × 900.

like *T. leptotes,* the plants initiated buds which did not mature. One bud was obtained from a plant which was cold-treated by being placed out-of-doors for about three months during the winter. This bud was collected while the plant was being cold treated.

Numerous meiotic irregularities were found in the material examined; univalents were present in a large number of cells, micro-nuclei occurred frequently, and chromatin bridges after anaphase I were common. The weather conditions to which the material was exposed may have led to the meiotic irregularities, and an examination of additional material will be necessary before any conclusions can be drawn concerning the frequency of irregularities in this species.

Some cells were found in which there were no apparent irregularities, and nine bivalents were observed at metaphase I (fig. 6).

It is not yet known whether the collections at hand are self-sterile or self-fertile.

TOWNSENDIA MONTANA M. E. Jones. Two collections of this species

were studied. The plants of Culture 35 (from Teton Mountains) were self-sterile. Nine bivalents were observed at metaphase I (fig. 7), and no irregularities were found in microsporogenesis. Root-tip material of this collection also was examined and 18 chromosomes were observed (fig. 15).

An examination of microsporogenesis in plants of Culture 29 (from Wallowa Mountains) showed that they are tetraploid with $2n = 36$ (fig. 8). Although the chromosomes were frequently clumped, they were never found associated as bivalents. In prophase, as early as chromosomes were distinctly visible, only univalents were seen.

Generally there was only one meiotic division in this material. After this division cytokinesis took place, and a diad of microspores resulted. The two microspores split apart shortly after cytokinesis. Occasionally three nuclei resulted from meiosis, and when this happened one of the nuclei was often smaller than the other two. Tetrads of microspores also were formed, but they were uncommon.

Evidence which indicates that these plants are apomictic was obtained. This evidence is presented in a later section.

On several minor morphological characters plants of Culture 29 differ from those of Culture 35. Further studies may show that the two collections represent separate varieties or species on both cytogenetic and morphological grounds.

Townsendia Parryi Eaton. Three collections of this species were studied. Both diploid and tetraploid forms are represented in the collections.

Culture 31 was collected when the plants were not in flower and only two plants were obtained. These plants were self-sterile. Nine bivalents were observed at metaphase I (fig. 9), and no irregularities were found in microsporogenesis.

Cultures 8 and 34 are tetraploid with $2n = 36$ (fig. 10). As in tetraploid *T. montana,* the chromosomes were not paired at meiosis. Chromosome clumps also occurred frequently. In contrast to tetraploid *T. montana,* in which the microspores were formed in diads, tetrads of microspores regularly were formed in *T. Parryi.*

Cultures 8 and 34, like the collections of *T. grandiflora,* required a longer period to reach maturity than most other species. The first heads were produced on some plants about eight months after seed germination. Other plants of these collections required an even longer period for development. The plants flowered for a period of from two to four months, then died.

Evidence that the two tetraploid collections of this species are apomictic was obtained and is presented in a later section.

Townsendia incana Nutt. Two collections of this species were studied. Plants of Culture 6 produced their first heads about four months after germination. Greenhouse plants which started flowering in March, 1952, have flowered continuously up to the present. Meiosis in this culture was found so irregular that no pollen-mother-cell chromosome count

was made. As many as nine bivalents were seen in some cells, but in addition there were univalents and chromosome clumps which could not be analyzed.

In an examination of root tips, the chromosome count 2n=28 (fig. 12) was obtained. This number is at variance with what would be expected in a polyploid series with a base number of nine, and it is likely that the collection represents a group of plants which are triploid with one extra chromosome. Evidence to support this hypothesis is outlined as follows:

1. The taxon is very similar morphologically to other taxa in the genus which have a base number of nine. It is especially close to *T. arizonica*.
2. Another triploid collection has been found in the genus.
3. Both bivalents (nine were seen in one cell) and univalents are found in the same pollen mother cell.
4. Evidence that the plants are apomictic was obtained.
5. In apomicts the abnormal chromosome complement would offer no difficulties in reproduction.

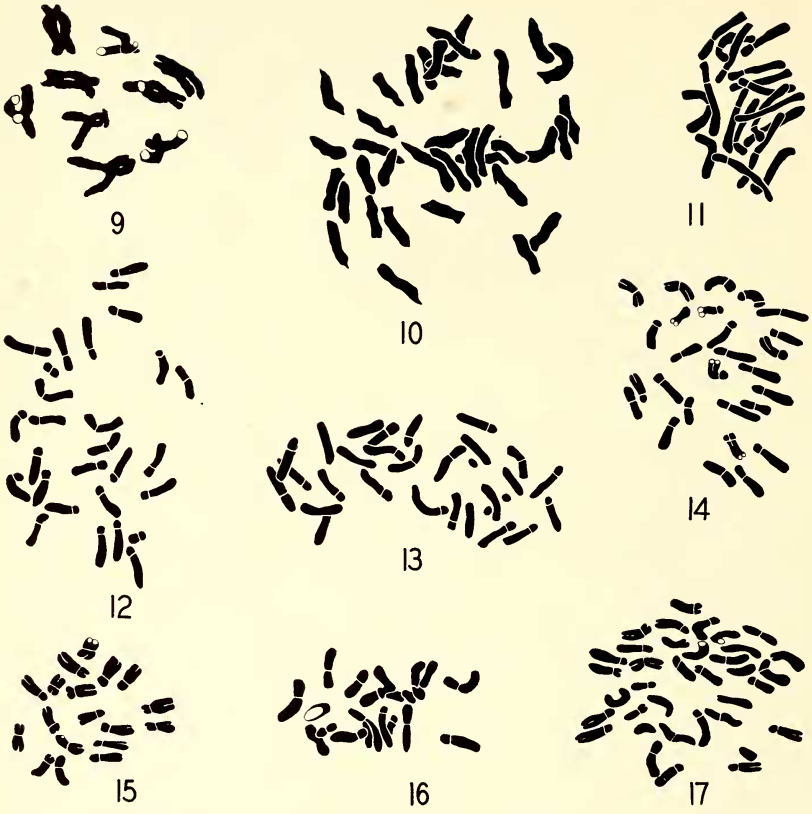
If the plants are of triploid constitution, it is also likely that they are alloploids. Evidence for alloploidy is found in the mitotic karyotype (fig. 12) where two chromosomes are conspicuously shorter than the others. These two chromosomes probably represent an homologous pair from two similar genomes. The absence of a third short chromosome suggests that the third genome is different from the other two and has been introduced through hybridization.

Culture 37 of *T. incana* was transplanted from the field. A study of microsporogenesis was made from buds collected both in the field and in the greenhouse. However, no accurate chromosome count was obtained because of chromosome clumping. As in the tetraploid *T. montana* and *T. Parryi* collections, there was no indication of chromosome pairing. Although asynapsis appeared complete, chromatin bridges were observed after both anaphases I and II. Formation of bridges suggests that at least partial synapsis must occur. Further study is necessary for a more complete understanding.

In an examination of root tips, the chromosome count 2n = 30 (fig. 13) was obtained. This number, like 2n = 28, does not fit in a polyploid series based on nine. It is likely that the plants are triploid plus three extra chromosomes.

In contrast to Culture 6, plants of Culture 37 cannot readily be considered alloploids. In the karyotype of this collection (fig. 13), three very short chromosomes are apparent. These short chromosomes could indicate three similar genomes (autoploidy), or one of them could be a duplicated chromosome. If the latter is the case, alloploidy is still possible.

An interesting feature about plants of Culture 37 is that they produced no pollen. A fairly large number of microspores were found in the anthers shortly after the tetrads had broken apart. At later stages fewer and fewer microspores or pollen grains were found. By the time of anthesis, no pollen was observed, and the anthers had started drying up.



Figs. 9–10. Meiotic chromosomes of *Townsendia*. Fig. 9. *T. Parryi* (Culture 31). Fig. 10. *T. Parryi* (Culture 8). All × 900.

Figs. 11–17. Mitotic chromosomes of *Townsendia*. Fig. 11. *T. grandiflora* (Culture 39). Fig. 12. *T. incana* (Culture 6). Fig. 13. *T. incana* (Culture 37). Fig. 14. *T. minima* (Culture 3). Fig. 15. *T. montana* (Culture 35). Fig. 16. *T. exscapa* (Culture 46). Fig. 17. *T. Rothrockii* (Culture 44). All × 900.

Evidence indicating that the plants of the two collections of *T. incana* are apomictic is presented in a later section.

Townsendia minima Eastwood. One collection of this species was studied. These plants, like those of *T. leptotes* and *T. mensana,* initiated buds which did not mature. A three-months cold treatment during the winter was used to induce flowering.

In an examination of microsporogenesis, meiosis was found so irregular that no chromosome count could be made. Most of the chromosomes were badly clumped, but in some pollen mother cells bivalents and univalents were seen. In an examination of root tips it was found that the plants are triploid with $2n = 27$ (fig. 14).

Evidence indicating that the plants of this collection are apomictic is presented in a later section.

Other species studied. In the following species, no buds were available for studies of microsporogenesis, and chromosome counts were made from root-tip preparations. These species with their culture number and chromosome number are: *Townsendia exscapa* (Rich.) Porter, Culture 46, 2n = 18 (fig. 16); *Townsendia Rothrockii* A. Gray, Culture 44, 2n = 36 (fig. 17); and *Townsendia spathulata* Nutt., Culture 47, 2n = 36 (?). A further study of these species is planned when buds become available.

Apomixis

Heiser (1948) first suggested the possibility of apomixis in *Townsendia*. In examining herbarium specimens of *T. scapigera*, he noted two very different population complexes in California. He found that specimens from Inyo County were dwarf plants, while those from the Sweetwater Mountains were large. In this connection, he stated: "Examination of the pollen of the latter [Sweetwater Mountains] specimens revealed a high percentage of empty grains, as well as the presence of both 3- and 4-pored grains similar to those found in many apomictic species."

During the course of the present study, apomixis was first suspected to be one of the mechanisms of reproduction in *Townsendia* when study of microsporogenesis in tetraploid *T. Parryi* (Culture 8) showed the chromosomes to be completely asynaptic; that is, only univalents were found at meiosis. Plants of this culture were found to produce large quantities of viable seeds even after cross-pollination was prevented. Because of the asynaptic condition it was concluded that these seeds were produced apomictically rather than as a result of fertilization. Diploid plants with regular pairing produced few or no seeds when cross-pollination was prevented. Thus in *Townsendia*, production of many viable seeds by non-cross-pollinated plants may be considered to suggest apomixis in those plants.

Since the first observation of asynapsis in *T. Parryi*, partial or complete asynapsis has been found in plants of six other collections. These collections are: *T. incana*, Culture 6; *T. incana*, Culture 37; *T. mensana*, Culture 38; *T. minima*, Culture 3; *T. montana*, Culture 29; and *T. Parryi*, Culture 34. With the exception of *T. mensana* (which has not been tested) non-cross-pollinated plants of these collections produced viable seeds. It also was found that these plants produce a uniform progeny. The presence of asynapsis, the production of viable seeds without cross-pollination, and the production of a uniform progeny strongly suggest apomixis in these collections.

Further evidence for apomixis in two collections (*T. Parryi*, Culture 8 and *T. incana*, Culture 6) was obtained by means of a rather simple experiment. Heads were treated by removing the corolla, stamens, and style from each disk floret. The ray florets likewise had the corollas and styles removed. This treatment was made before pollen in any of the florets had turned yellow. Development of the achenes was apparently normal in spite of the treatment, and there was a high percentage of viability of the seeds.

In order to correlate pollen quality with apomixis and sexuality in the genus, a study of the pollen of several apomicts and several sexual species was made. In Table 2 the quality of pollen from one plant of each of these cultures is shown. The pollen quality in the apomicts is very low in comparison to that of the sexual species and provides additional evidence that seed formation in some species of the genus must be possible without fertilization.

Five lines of evidence indicating apomixis in *Townsendia* may be summarized as follows:

1. Asynapsis.
2. Production of many viable seeds by non-cross-pollinated plants.
3. Production of a uniform progeny.
4. Seed development in spite of removal of stamens and styles from florets.
5. Low pollen quality.

During the study of pollen quality, it was observed that the pollen-grain size for each species was relatively constant. Diameter measurements of fresh pollen grains were therefore made. Twenty-five good (as defined in Table 2) pollen grains from one plant of each species were

Table 2. Comparison of Pollen Quality and Size of Some Apomicts and Sexual Species.

Taxon	Culture	No. of grains counted	No. of good* grains	Per cent of good* grains	Mean diam. of good* grains in microns	Standard deviation
Apomictic						
T. incana	6	358	45	12.6	48.1	± 1.8
T. incana	37	no pollen produced†		.....	.....	.....
T. minima	3	379	69	18.2	38.9	± 0.8
T. montana	29	329	4	1.2	43.1	± 5.6
T. Parryi	8	352	225	63.9	46.0	± 2.7
Sexual						
T. anomala	33	466	458	98.3	23.6	± 1.5
T. arizonica	5	376	368	97.9	28.9	± 1.3
T. florifer	1	372	359	96.5	26.7	± 1.5
T. leptotes	42	393	377	95.9	26.5	± 0.9
T. mensana	38	484	412	85.1	23.5	± 1.2
T. montana	35	348	332	95.4	25.8	± 1.1
T. Parryi	31	387	384	99.2	26.3	± 1.5

* If a nucleus, or nuclei, could be seen in a grain after it was stained for one hour in aceto-carmine, it was considered good.

† See under discussion of *T. incana,* Culture 37.

measured. The spicules were not included in the measurements. An ocular micrometer and 900 times magnification were used for measuring. The mean diameter and standard deviation in microns of the pollen grains of each species studied are given in Table 2.

The tabulations of pollen quality and size show some very striking differences between the apomicts and the sexual species. The knowledge of these differences should be useful in subsequent studies when it may be

Table 3. Comparison of Pollen Quality of Hybrids With That of the Parents

Taxon	No. of grains counted	No. of good* grains	Per cent of good* grains
T. arizonica × *T. florifer*	685	360	52.6
T. florifer × *T. arizonica*	664	223	33.6
T. arizonica	376	368	97.9
T. florifer	372	359	96.5

* If a nucleus, or nuclei, could be seen in a grain after it was stained for one hour in aceto-carmine, it was considered good.

necessary to distinguish between apomictic and sexual plants on the basis of pollen from herbarium specimens.

A study of the embryology of *Townsendia* should be very helpful in understanding apomixis in the genus. No work along this line has been attempted, but embryological studies are planned as a future project.

Interspecific Hybridization

Cross pollinations have been made among several diploid, self-sterile species, but this work is only in its preliminary stages. Extensive crossing, involving sexual species and the apomicts as well, is planned as a future project. Hybridization experiments should yield information concerning apomixis, natural relationships, and evolution within the genus.

Small quantities of apparently viable seeds were obtained from the crosses listed below and their reciprocals:

T. anomala (Culture 33) × *T. arizonica* (Culture 5)
T. anomala (Culture 33) × *T. montana* (Culture 35)
T. arizonica (Culture 5) × *T. florifer* (Culture 1)
T. arizonica (Culture 5) × *T. montana* (Culture 35)
T. arizonica (Culture 5) × *T. Parryi* (Culture 31)
T. florifer (Culture 1) × *T. montana* (Culture 35)
T. florifer (Culture 1) × *T. Parryi* (Culture 31)
T. montana (Culture 35) × *T. Parryi* (Culture 31).

One hybrid plant, *T. arizonica* × *T. florifer,* and one plant of the reciprocal were grown to maturity. The two plants were similar morphologically and intermediate between the parents.

Study of meiosis in the hybrids revealed no irregularities. Chromosome pairing was apparently as regular in them as in the parents. In contrast to this lack of difference at meiosis, an examination of pollen of the hybrids and the parents revealed a very significant difference in their pollen qualities. This difference is shown in Table 3.

Summary

Cytogenetic studies were made in thirteen species of *Townsendia,* represented by twenty collections. Chromosome counts were obtained from studies of microsporogenesis and from examination of root tips. The chromosome numbers $2n = 18$, $2n = 27$, $2n = 28$, $2n = 30$, and $2n = 36$ were found in the genus. It is concluded that the base number is nine.

In the diploid collections, which are self-sterile, meiosis is usually regular, with nine bivalents at metaphase I, and pollen quality is high. In four polyploids, meiosis is irregular with univalent formation up to complete asynapsis, chromatin bridges, and the occurrence of only one meiotic division in microsporogenesis. These polyploids were found to be apomictic. Characteristically they form unreduced pollen through failure of synapsis and may be detected by their poor pollen quality and ability to set seed without cross pollination. Removal of stamens and styles from florets at an early stage did not prevent production of viable seeds. The pollen grains of the polyploids are distinctly larger than those of the diploids.

Hybrid seeds were obtained from cross pollination of several diploid, self-sterile species. One hybrid plant, *T. arizonica* × *T. florifer*, and one plant of the reciprocal were grown to maturity. Chromosome pairing was found as regular in the hybrids as in the parents, but hybrid pollen quality was low.

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BRYOPHYTA OF SANTA CATALINA ISLAND, CALIFORNIA

William C. Steere

Like most insular floras, that of Santa Catalina Island has attracted a large amount of botanical attention which, of course, has been stimulated by the high degree of endemism there. The comprehensive survey of the flora by Millspaugh and Nuttall (1923) covers all groups of plants, including the Bryophyta, and reviews the older literature. A more recent paper by Sayre (1940) lists the mosses collected by T. D. A. Cockerell (1938) on Santa Catalina Island, as well as on other islands off the coast of California. Some of the records cited by Millspaugh and Nuttall, as well as new collections, are included in the standard manuals of American mosses and hepatics (Grout, 1928–1940; Frye and Clark, 1937–1948) and by Koch (1950) in his check-list of the mosses of the state of California. In these several works we find eight species of Hepaticae and approximately thirty species of Musci reported definitely from Santa Catalina Island.

During the annual field meeting held jointly by the California Botani-